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THE CENTRAL NERVOUS SYSTEM AS A FACTOR IN THE REGENERATION OF POLYCLAD TURBELLARIA.

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Some years ago L. V. Morgan¹ described a series of experiments concerning the effect of removal of the cephalic ganglia upon the course of regeneration, particularly of the anterior region, in the Californian polyclad, *Leptoplana littoralis*. Her conclusion is that under certain conditions, *i. e.*, particularly in the presence of tissue anterior to the ganglia, regeneration occurs as readily and as completely in the absence of the ganglia as when they are present. At about the same time the results of my own experiments on *Leptoplana tremellaris* appeared.² I found that when half or less than half of the ganglionic tissue was removed, regeneration might be as complete and as rapid as when the ganglia were uninjured, but that when more than half of the ganglia was removed, regeneration was not only slower but less complete than when they were uninjured.

I also found, however, that groups of eye spots not infrequently appeared in cases where the ganglia themselves were, so far as could be determined, completely removed, and that the amount of anterior new tissue in all such cases was greater than in those cases where eye spots did not appear, though regeneration was never complete.³ My general conclusion from these experiments was that the central nervous system in these forms acted as a functional stimulus to the growth of new tissue, increasing both the rapidity and the amount of growth.

The above mentioned experiments of L. V. Morgan seem to

¹L. V. Morgan, "Incomplete Anterior Regeneration in the Absence of the Brain in *Leptoplana littoralis*," *Biol. Bull.*, IX., 3, 1905.

²Child, "Studies on Regulation, "V.—The Relation between the Central Nervous System and Regeneration in *Leptoplana*: Posterior Regeneration," *Journ. Exp. Zool.*, I., 3, 1904. "Studies on Regulation, VI.—The Relation, etc.: Anterior and Lateral Regeneration," *Journ. Exp. Zool.*, I., 4, 1904.

³Child, "Studies on Regulation, VI.," Figs. 15-19, p. 522, Figs. 41-43, p. 526, also p. 529.

indicate that under certain conditions this is not the case. In view of the apparent disagreement between her results and my own further experiment seemed desirable and during the autumn of 1907 and the summer of 1910 I took the opportunity to examine several species of Leptoplanidæ which occur at La Jolla, Calif., with reference to this point. In 1905 I had worked with *L. littoralis* at Pacific Grove and obtained results similar to those described for *L. tremellaris*.

My conclusions from this later work are essentially the same as those reached in my earlier paper. Removal of the ganglia with as little of the surrounding tissue as possible always results in decreased rapidity and completeness of regeneration, whatever the method of operation employed. In many cases, however, groups of eye spots appear in the new tissue, even when the ganglia are wholly absent, and in such cases the regeneration is always more rapid and more nearly complete than when the eye spots do not appear.

When the ganglia are removed by a cut from one side of the head, as in some of Morgan's experiments, more new tissue is often formed, or it forms more rapidly, in the deep cleft made by the cuts than on a nearly flat terminal surface. This, however, is not due to any specific effect of the anterior tissue, but is merely a very general characteristic of wound-healing, not only in *Turbellaria*, but in many other forms, and is doubtless due to the fact that nutritive and other conditions for growth are better in such a cleft, where the growing parts are in contact on both sides with other tissue, than on surfaces where such contact exists only on one side.

I believe that the important point in connection with the problem of the influence of the central nervous system on regeneration in these forms lies in the question as to what constitutes the central nervous system. As Morgan states, the cephalic ganglia in the polyclads are enclosed in a definite sheath, but a further point of great importance which she does not consider at all is that the nerve roots contain numerous ganglion cells for a considerable distance from their point of origin in the ganglia. Reference to Lang's monograph of the polyclads¹ is sufficient to

¹Lang, "Die Polycladen des Golfes von Neapel," *Fauna und Flora des Golfes von Neapel*, XI., Leipzig, 1884.

establish this point. There is then every reason to believe that the central nervous system comprises, not the ganglia alone, but the ganglia plus the nerve roots for a certain greater or less distance from their origin. Even when the ganglia are completely removed, the capacities of the central nervous system for regeneration and stimulation are not wholly lost, if sufficient portions of the nerve roots near the ganglia remain. In such cases the amount of regeneration is greater than when the nerve roots are also removed, and groups of eye spots may appear. In fact, in one case¹ I observed the regeneration of a small but distinct ganglionic mass after the apparently complete removal of the ganglia. It seems not improbable that if our technique were sufficiently exact to permit removal of the ganglia without injury to the nerve roots except at their origin, the regeneration even of the ganglia themselves, as well as of other parts, might be almost or quite as complete as when the ganglia remain.

L. V. Morgan's Fig. B2 of the regenerated anterior end of the nervous system after removal of the ganglia shows only fibrillar structure and she states that only fibrillæ are present in the mass. But when we recall the facts as to the histological structure of the nerve roots it seems extremely improbable that ganglion cells are totally absent from such regenerated masses. In all cases of the kind, which I have observed, some cells as well as the fibrillæ have always been present in the knot of tissue formed by the union of the nerve roots.

The development of eye spots in many of the cases without ganglia described by Morgan is undoubtedly due to regenerative processes in the remaining ganglionic nerve roots. In my own experiments I have found that in all cases, whatever the method of operation, where the ganglia plus a sufficient portion of the nerve roots are removed the regeneration is always slight, eye spots do not develop and the animal never shows any recovery from its sluggish unresponsive condition, *i. e.*, it behaves in all respects like a headless animal. On the other hand, where the roots are largely intact, regeneration is more rapid and proceeds farther, eye spots often appear and the recovery of motor activity and apparent spontaneity frequently occurs to a very marked extent.

¹Child, "Studies, etc., VI.," Fig. 43, p. 526.

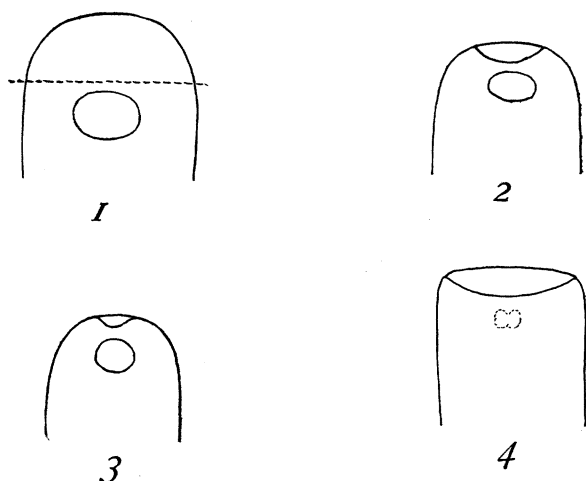
Since my later experiments confirm in all respects my earlier work, it seems unnecessary to describe them in detail and to figure all the various methods of operation and the results. I can only conclude that the apparent absence of effect of ganglionic removal upon regeneration in certain cases is due to one of two things, viz., failure to remove the ganglia completely, or the presence of the intact nerve roots. Morgan's experiments do not in any way prove that the central nervous system does not exert an influence upon the rapidity and amount, and so far as the sense organs are concerned, upon the character of regeneration in the polyclads.

As regards one point, however, Morgan's results as stated in her paper disagree so completely with my own that some further consideration is necessary. In the concluding paragraph of her paper the statement appears that "regeneration of the anterior tip of the worm, that is when the worm has been cut off anterior to the ganglia, occurs in the absence of the ganglia as well as when they are present." Individuals with the ganglia removed and the end cut off anterior to the ganglionic region regenerated as rapidly and completely as controls with uninjured ganglia and the anterior end cut off at the same level. In these experiments the ganglia were removed by using the cut end of a straw as a punch and after the wound thus made had healed the anterior region of the head was cut off.

I have performed this experiment a large number of times and on various species of *Leptoplanidæ* and with essentially uniform results, viz., that in all cases where the ganglia were actually completely removed, regeneration was less rapid and less complete than in control experiments with uninjured ganglia. Moreover the larger the portion of the nerve roots removed in addition to the ganglia themselves, the less rapid and less complete the regeneration. The operation is by no means easy to perform successfully and in many cases larger or smaller portions of the ganglia remain: such cases show all gradations from complete regeneration to a condition essentially like the pieces from which the ganglia are totally absent, but they must of course be regarded as unsuccessful experiments for our present purpose.

In my experiments the ganglia were removed with a straw in

the manner described above: two weeks later, after the wound had completely healed and the ganglionic region was filled in with new tissue, the anterior end of the head region was removed by a cut as indicated in Fig. 1. At the same time the anterior ends were removed at the same level from another series of individuals with uninjured ganglia.



FIGS. 1-4.

The condition of the animals without ganglia a week after the second operation is indicated in Figs. 2 and 3, while Fig. 4 shows the condition of the controls. The difference is marked and requires no comment. After two weeks more regeneration is almost or quite complete in the controls, while the animals without ganglia remain essentially as before and regeneration never proceeds further in them.

In these experiments great care was used to be certain that the ganglia were entirely removed. In various species the ganglia can be seen quite clearly from the ventral surface and examination from this side after the operation will usually show even rather small pieces of the ganglia if they remain. Morgan does not state how the total absence of the ganglia was determined in her experiments and it seems probable that in cases where the anterior end of the head regenerated as rapidly and as completely in animals supposedly without ganglia as in those with uninjured

ganglia some portions of the ganglia remained. It is possible that in some cases where the nerve roots were largely intact regeneration might be almost as rapid and complete as when the ganglia are present, but it is certainly impossible to make an extensive series of operations which are uniform in this respect. Morgan's experiments of this kind included however, only "several" worms.

The only conclusion possible seems to be then that the central nervous system, *i. e.*, the nerve roots near their origin from the ganglia, as well as the ganglia themselves, do affect in marked degree the rapidity and amount of regeneration of the anterior regions and, at least as regards the sense organs, its character as well. Moreover, where the ganglia, or the ganglia together with the nerve roots, are removed the method of operation makes no essential difference in the result. As most experiments, not only on the turbellaria but on other forms, indicate, it is probable that the early stages of the formation of new tissue are largely or wholly independent of the nervous system, but it is difficult to understand how the nervous system of an adult animal could fail to affect the amount and rapidity of growth in a regenerating part composed largely of muscles and sense organs. Absence of such an affect would be in direct opposition to the well established fact of the functional influence of the nervous system on various parts of the organism. The rate of metabolism and consequently the rate of growth—*i. e.*, provided nutritive material is present—in such parts must be in greater or less degree dependent upon nerve stimuli. Such an influence of the nervous system upon growth must, however, be sharply distinguished from the determination of differentiation of parts: the effect of the functional stimulus in the stricter sense is primarily quantitative rather than qualitative, so far as structure is concerned. These points were emphasized in my earlier papers.

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